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A CYTOTAXONOMIC STUDY OF THE GENUS HYMENOPAPPUS (COMPOSITAE)[1]

BILLIE L. TURNER

Hymenopappus, an exclusively North American genus, has its greatest concentration of species in the United States. It has been conventionally placed in the tribe Helenieae of the family Compositae, a group of plants which is almost entirely North and South American. Of the 55 genera recognized for the tribe by Hoffmann (1897) in Engler and Prantl, only 3 occur on other continents. Thus the members of Helenieae should serve as excellent genera for monographic and evolutionary studies by American taxonomists, particularly since a considerable amount of the available herbarium material, including many types, may be obtained in this country. Equally, if not more important, is the opportunity for extensive field and cytogenetic work with members of the group. The genera in the tribe seem good subjects for chromosomal studies since both pollen mother-cell smears and root-tip squashes are easily made and excellent results are obtained. Since the naturalness of the tribe has been seriously questioned by Small (1919, p. 312) and more recently by Cronquist (1955), the accumulation of detailed knowledge of the included genera, particularly of evolutionary trends and chromosomal studies, is especially desirable.

Comparatively few genera of the Helenieae have been studied

[1] Part of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the State College of Washington. Post-doctoral field work was supported in part by the Plant Research Institute of the University of Texas.

monographically, much less cytotaxonomically, in recent years.[2] The completion of a larger number of such studies, combined with information from other tribes, particularly the Heliantheae, should provide much evidence on the affinities of the included genera and on the naturalness of the tribe as a whole.

In addition to this larger aspect of plant phylogeny and evolution, there are many problems at the specific level. Several genera of this tribe have occasioned considerable taxonomic confusion, particularly in the United States and Mexico. *Hymenopappus* is such a genus. The natural groups of this taxon have been treated in various ways. Gray (1886) recognized 7 species; Rydberg (1914), 28 species (including three of *Hymenothrix*); Johnston (1923), 14 species and one variety. The present account recognizes 25 taxa: 10 species, and 15 varieties (including one new species, and three new varieties).

Most of the shuffling and reshuffling of names has been in the *H. filifolius* complex, a group of closely related taxa distributed principally in the Rocky Mountains, Great Basin, and adjacent plains and deserts. These infraspecific units (as treated in the present paper) occupy more or less distinct habitats and are, for the most part, allopatric, although considerable overlap and intergradation often occurs peripherally with closely related taxa. This intergradation, combined with much spatial (but not altitudinal or ecological) overlap, has made the assembling of a great deal of herbarium material, seed for garden studies, and first hand field knowledge an absolute necessity for the understanding of the complex. The present treatment is an attempt to bring together this information so as to clarify many of the existing problems, as well as to show the relationships of the more easily recognized members of the genus. In general, the most valuable part of this information, aside from that obtained from herbarium specimens, has been obtained from field work and uniform garden cultures. Acquaintance with local and regional populations, their habitats, variability, and ranges, combined with later responses of representative individuals in the garden, has been invaluable. Chromosomal

[2] The following have been monographed or revised since 1930: *Chaenactis* (Stockwell, 1940); *Eriophyllum* (Constance, 1937); *Gaillardia* (Biddulph, 1944); *Hymenoxys* (Parker, unpubl.); *Monolopia* (Crum, 1940); *Palafoxia* (Baltzer, 1944); *Perityle* (Everly, 1947); *Schkuhria* (Heiser, 1945).

information has proved to be significant in relatively few taxa, though much remains to be done along this line, particularly in the *H. filifolius* var. *lugens* complex.

In some cases the problems raised by the author are more complex than those he attempted to solve, but remaining problems are few, and it is believed that the present treatment to a large extent places the individuals in natural groups from the standpoint of morphology, geography, ecology, and probably phylogeny.

Historical Account

The genus *Hymenopappus* was proposed by L'Heritier in 1788 to accommodate *H. scabiosaeus*, a species grown from seed that had been collected in Carolina by Michaux and sent to Europe. The original publication consisted of only three pages, one of these being a plate.[3] Three years later Lamarck (1792) unaware of L'Heritier's description, redescribed the genus as *Rothia*, basing his name *R. caroliniensis* also on plants grown from seed collected by Michaux in Carolina.[4]

From 1788 until Gray (1886) treated the group in his Synoptical Flora of North America, seven of the ten species recognized in the present paper were described (one of these was included in the genus *Leucampyx*). Though Gray did not group the species of the genus into series, he clearly pointed out the distinctions of these groups in his key to species.

After Gray's treatment a number of new species were proposed; nearly all of these fell into the immediate vicinity of *H. filifolius*, a highly variable species-complex of the western United States. This period was climaxed by Rydberg (1914) who described four new species for the genus and recognized, in all, 28 species and no varieties. In addition, he confused generic limits by transferring three species of *Hymenothrix* to *Hymenopappus*.

[3] According to Britton and Woodward (1905) only a few of these sets ("monographs") were circulated, probably no more than five or twelve. In connection with the present study, two copies have been located, one in the library of the Linnaean Society in London, and the other in the library of the New York Botanical Garden.

[4] Kuntze (1891) thought that L'Heritier's genus did not appear until 1803, and argued that *Rothia* Lam. is the older name. Britton and Woodward (1905) give 1788 as the probable date for *Hymenopappus*. Since the generic name *Rothia* was already preoccupied at the time of Lamarck's publication, according to the International Code of Botanical Nomenclature (1952), *Hymenopappus* is the name to be used for the genus whether the date 1788 is correct or not.

Johnston (1923) gave a brief account of the genus in which he reduced most of the obvious relatives of *H. filifolius* to synonymy under that species. In many respects Johnston's treatment was like that of Gray, with the important exceptions of the reduction of *Leucampyx* to synonymy under *Hymenopappus* and the retention of *Hymenothrix palmeri* within the genus. The present treatment, at the specific level, is also like Gray's, but with several notable exceptions: *Leucampyx* is placed in synonymy under *Hymenopappus;* three species described as new since his time are considered to be valid; and *H. filifolius* has been treated as a species-complex composed of a number of recognizable geographic variants. In this latter respect this treatment is like that of Rydberg, most of his species being considered varieties in this paper. In addition, for the first time, a clear morphological distinction has been made between the genera *Hymenothrix* and *Hymenopappus.*

Chromosomal Studies

Because of the apparent variability and wide distribution of the members of the genus *Hymenopappus,* it was thought early in this study that chromosomal information might be of considerable help in unraveling taxonomic problems. It soon became apparent, however, that the number $n = 17$ was constant for nearly all members of the genus, the exceptions being two tetraploid varieties or races within the *H. filifolius* complex.

Methods.—Collections of buds and/or seeds for chromosomal studies were made in the field during the summer of 1951.[5] Two different treatments were used for killing and fixing buds: either they were killed and fixed in Belling's modified Navashin's fluid directly (after removal of enclosing bracts), or they were fixed in Carnoy's fluid (9 parts absolute ethyl alcohol: 3 parts glacial acetic acid: 1 part chloroform) for 10 minutes then transferred to Navashin's fluid, a procedure suggested by Johansen (1940, p. 33). Buds collected in this manner were passed through a tertiary butyl alcohol series and embedded in paraffin. Sections were made at 15–20 microns, and the material stained with crystal violet. Prefixing of the material in Carnoy's

[5] Voucher specimens are deposited in the herbarium of the State College of Washington; collections made during 1954 and 1955 are in the University of Texas Herbarium.

fluid before transferring to Navashin's fluid gave best results, though, in general, neither treatment was very satisfactory for meiotic chromosomal studies. The bivalents tended to clump tightly together at metaphase obscuring individual chromosomes, although when meiotic material was found at late prophase good results were obtained.

Seeds collected in the field were grown in a uniform garden and pollen mother cell smears were made from these plants. Though the species of *Hymenopappus* are perennial and biennial, it was found that by germinating the seeds in the greenhouse during December and January and transplanting to the garden in spring, flowering could be induced the same year. Seeds germinated after January usually produced only rosettes the first year. Freshly collected buds from garden plants were placed on slides and the anthers removed to a drop of aceto-carmine where they were macerated with a glass rod. Since the chromosomes tended to clump at metaphase of meiosis, considerable pressure on the cover slip was required to spread them sufficiently for counting. Less pressure is needed at late prophase, and most of the counts and drawings were made at this stage. In addition to smearing fresh material directly, buds were also fixed in a modified Carnoy's fluid (4 parts chloroform: 3 parts absolute alcohol: 1 part glacial acetic acid) and stored under refrigeration, a method suggested by Walters (1952). Material collected in this manner takes a better stain with acetocarmine than does similarly stained fresh material. Buds may be stored for at least six months in the fluid with good results, and probably much longer.

Attempts to obtain counts and to determine chromosome morphology from root-tip material by standard embedding techniques was not rewarding. The root-tip chromosomes are extremely long, and because of their number ($2n = 34$), the metaphase plates appeared as a mass of interwoven chromosomes. However, excellent results were obtained in the latter part of this study through the use of a method suggested by Speese and Baldwin (1952). Seeds were germinated on moist filter paper and the primary radicles excised after they had emerged about 6 mm. These were placed in a saturated aqueous solution of paradichlorobenzene for two hours, washed in distilled

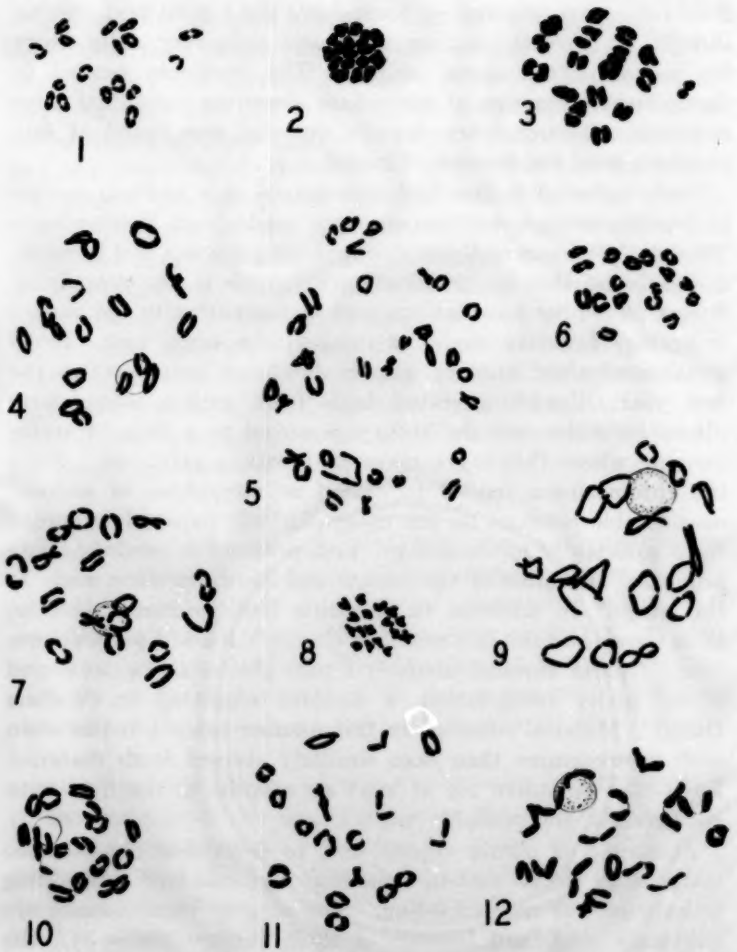


Fig. 1–12. Meiotic chromosomes of *Hymenopappus* species. Fig. 1. *H. filifolius* var. *parvulus* (*P. & T. 2802*). Fig. 2. Same, first metaphase, crystal violet preparation. Fig. 3. *H. f.* var. *filifolius* (*P. & T. 2293*). Fig. 4. *H. f.* var. *nanus* (*P. & T. 2608*). Fig. 5. *H. f.* var. *lugens*, white-flowered tetraploid race (*P. & T. 2666*). Fig. 6. Same, yellow-flowered diploid race (*P. & T. 2504*). Fig. 7. *H. newberryi* (*T. 2894*). Fig. 8. Same, second metaphase. Fig. 9. *H. filifolius* var. *cinereus* (*P. & T. 2830*). Fig. 10. *H. flavescens* var. *canotomentosus* (*P. & T. 2670*). Fig. 11. *H. tenuifolius* (*T. 2895*). Fig. 12. *H. scabiosaeus* var. *corymbosus* (S.V.F.). All × ca. 1000.

FIG. 13–20. Mitotic chromosomes of *Hymenopappus* species. Fig. 13. *H. filifolius* var. *cinereus* (*P. & T. 2754*). Fig. 14. *H. flavescens* var. *flavescens* (*Warnock;* Crane Co., Texas). Fig. 15. *H. filifolius* var. *nanus* (*P. & T. 2608*). Fig. 16. *H. f.* var. *lugens*, yellow-flowered diploid race (*P. & T. 2645*). Fig. 17. *H. f.* var. *luteus* (*P. & T. 2872*). Fig. 18. *H. f.* var. *polycephalus* (*S.V.F.;* Golden, Colorado). Fig. 19. *H. f.* var. *cinereus* (*P. & T. 2751*). Fig. 20. Same, chromosome set aligned and traced from Fig. 21. All × ca. 1250.

TAXON	SOURCE	Chromosome Number P.M.C.	Root Tip
H. artemisiaefolius var. *artemisiaefolius*	TEXAS. Kleberg Co.: eastern Laureles Division of King Ranch, *M. C. Johnston 54411.* (This plant somewhat intermediate to *H. a.* var. *riograndensis*).	17	
	TEXAS. Colorado Co.: 5 mi. N.W. of Columbus, *Turner 3361.*	17	
H. artemisiaefolius var. *riograndensis*	TEXAS. Kleberg Co.: S. end of Canelo Pasture, Santa Gertrudis Division of King Ranch, *M. C. Johnston 54483.*	17	
	TEXAS. Hidalgo Co.: 5 mi. S. of Brooks County line, U. S. Highway 281, *M. C. Johnston 54528.*	17	
H. filifolius var. *cinereus*	COLORADO. Boulder Co.: 6 mi. N. of Boulder. *Q. Jones 835.*		34
	*COLORADO. Chaffe Co.: 4 mi. W. of Salida, *Preece & Turner 2830.*	17	
	COLORADO. Gunnison Co.: Cimarron, *Preece & Turner 2793.*		34
	COLORADO. La Plata Co.: 1 mi. N. of Durango, *Preece & Turner 2754.*		34
	NEW MEXICO. Sandoval Co.: 7 mi. N.W. of Cuba, *Preece & Turner 2751.*		34
	*NEW MEXICO. Santa Fe Co.: 3 mi. S.E. of Espanola, *Preece & Turner 2739.*	17	
	*NEW MEXICO. Santa Fe Co.: 4 mi. S. of Espanola, *Preece & Turner 2741.*	17	
H. filifolius var. *filifolius*	OREGON. Morrow Co.: 2 mi. W. of Boardman, *Ownbey & Preece 3366.*	17	
	OREGON. Wheeler Co.: 4 mi. E. of Mitchell, *Ownbey & Preece 3362.*	17	
	*WASHINGTON. Adams Co.: 12 mi. W.N.W. of Washtucna, *Turner 2293.*	17	34
H. filifolius var. *idahoensis*	IDAHO. Lemhi Co.: 14 mi. S. of Salmon, *Preece & Turner 2378.*	17	
H. filifolius var. *lugens*	*ARIZONA. Coconino Co.: 9 mi. E. of Peach Springs, *Preece & Turner 2610.*	17	
	*ARIZONA. Coconino Co.: 2 mi. E. of Ash Fork, *Preece & Turner 2618.*	34	
	ARIZONA. Coconino Co.: 7 mi. W. of Williams, *Preece & Turner 2628.*		68
	*ARIZONA. Coconino Co.: 10 mi. S. of Flagstaff, *Preece & Turner 2645.*	17	34
	*ARIZONA. Coconino Co.: 5 mi. E. of Flagstaff, *Preece & Turner 2666.*	34	
	*ARIZONA. Yavapai Co.: 5 mi. W. of Seligman, *Preece & Turner 2614.*	34	
	*NEW MEXICO. Catron Co.: 35 mi. N. of Alma, *Preece & Turner 2710.*	34	
	NEW MEXICO. Catron Co.: 15 mi. N. of Alma, *Preece & Turner 2711.*		68
	UTAH. Kane Co.: 3 mi. W. of Long Valley Junction, *Preece & Turner 2466.*	17	
	*UTAH. Kane Co.: 1 mi. S. of Glendale, *Preece & Turner 2504.*	17	

TAXON	SOURCE	Chromosome Number P.M.C.	Root Tip
H. filifolius var. *luteus*	*WYOMING. Sweetwater Co.: 32 mi. S. of Green River, *Preece & Turner 2872.*	17	34
H. filifolius var. *nanus*	*ARIZONA. Mohave Co.: 6 mi. E. of Peach Springs, *Preece & Turner 2608.*	17	34
	UTAH. Washington Co.: 7 mi. S.W. of Shivwits, *Preece & Turner 2558.*	17	
H. filifolius var. *nudipes*	UTAH. Kane Co.: 15 mi. N. of Orderville, *Preece & Turner 2499.*	17	
H. filifolius var. *parvulus*	*COLORADO. Gunnison Co.: 15.6 mi. W. of Gunnison, *Preece & Turner 2802.*	17	
	COLORADO. Saquache Co.: dry hills near Elko, *Preece & Turner 2816.*	17	
H. filifolius var. *pauciflorus*	ARIZONA. Coconino Co.: 20 mi. S.W. of Marble Canyon, *Turner 3066.*	17	
H. filifolius var. *polycephalus*	COLORADO. Jefferson Co.: Golden, July 12, 1951, *Rev. S. V. Fraser.*		68
	COLORADO. Larimer Co.: 1.5 mi. E. of Livermore, *Preece & Turner 2861.*	34	
H. filifolius var. *tomentosus*	UTAH. Washington Co.: Zion National Park, near lower entrance to road tunnel, *Turner 3065.*	17	
H. flavescens var. *cano-tomentosus*	*ARIZONA. Navajo Co.: 13 mi. S. of Holbrook, *Preece & Turner 2670.*	17	
	NEW MEXICO. Catron Co.: 8 mi. S.W. of Horse Springs, *Preece & Turner 2738.*	17	
H. flavescens var. *flavescens*	NEW MEXICO. Lea Co.: 2 mi. S. of Eunice, *Turner 2946.*		34
	*NEW MEXICO. Lea Co.: 5 mi. N. of Eunice, *Turner 2947.*		34
	*TEXAS. Crane Co.: sand between Crane and Odessa, June 15, 1952, *B. H. Warnock.*		34
H. mexicanus	ARIZONA. Coconino Co.: 10 mi. N. of Flagstaff, *Preece & Turner 2634.*	17	
	*ARIZONA. Coconino Co.: 4 mi. S. of Flagstaff, *Preece & Turner 2641.*		34
H. newberryi	COLORADO. Archuleta Co.: 1.5 mi. S.E. of Pagosa Springs, *Turner 2894.*	17	
	*NEW MEXICO. Sandoval Co.: Jemez Mts., 5 mi. S.E. of La Cueva, *Preece & Turner 2743.*	17	
H. radiatus	ARIZONA. Navajo Co.: 9.5 mi. N. of White River, *Preece & Turner 2686.*	17	
H. scabiosaeus var. *corymbosus*	*KANSAS. Cloud Co.: 2.5 mi. W. of Aurora, July 17, 1951, *Rev. S. V. Fraser.*	17	
	TEXAS. Austin Co.: 2.5 mi. N. of New Ulm, *Turner & Johnston 54333.*	17	
H. tenuifolius	NEW MEXICO. Santa Fe Co.: 14 mi. S. of Santa Fe, *Turner 2895.*	17	
	TEXAS. Coryell Co.: 3 mi. N. of Cooperas Cove, *Turner 3807.*	17	
	*TEXAS. Dallas Co.: Flagpole Hill, N. E. part of Dallas, *Beaman 519.*		34

* Collections grown in the garden are indicated by an asterisk (*).

water, and stored overnight in a modified Carnoy's fluid (3 absolute alcohol: 1 chloroform: 1 glacial acetic acid). Prior to squashing, the root-tips were hydrolyzed in acid alcohol (1 hydrochloric acid [sp. gr. 1.19]: 1 absolute alcohol) for 10–15 minutes and returned to the Carnoy's fluid. After 30 minutes to several hours the tips were removed and squashed in aceto-carmine. Staining of chromosomes was intensified when the slides were allowed to stand for one to three hours. Cover-slips were ringed with white Karo syrup for temporary mounts or made permanent by McClintock's method (1929).

Drawings were made with the aid of a camera lucida; in some instances mitotic chromosomes were spaced when these overlapped.

Results.—No previous chromosomal counts have been reported for *Hymenopappus*. In the following list counts are given for 20 of the 25 taxa, including eight of the ten species in the genus. All the species of the genus investigated were found to have the base number of $x = 17$. Two varieties of *H. filifolius* are tetraploid or have tetraploid races: var. *polycephalus* ($n = 34$), and var. *lugens* ($n = 17, 34$).

Meiotic chromosomes at late prophase are comparatively short with similar morphologies and nearly always with two terminalized chiasmata. In all the collections from which meiotic counts were made, pairing appeared normal except in some of the tetraploid races of *H. filifolius* var. *lugens* where two or three quadrivalents were found consistently (*Preece & Turner 2614, 2618, 2666*).

Mitotic chromosomes are more distinctive, showing conspicuous differences in both length and centromere position. One chromosome pair with extended satellites is particularly outstanding, and has been found in the somatic cells of all collections of *Hymenopappus* so far examined. No attempt has been made to make extensive chromosomal comparisons within the genus, and it is possible that such study might reveal significant karyologic differences among the taxa.

Though chromosomal studies have not been of much help in showing relationships or affinities within *Hymenopappus*, they have shown that the members of the genus are held together naturally. This is particularly interesting with respect to

H. newberryi which was originally described as a different genus and placed in a separate tribe (Anthemideae). In the light of the chromosomal as well as morphologic evidence, there can be little doubt now that the species is properly placed in *Hymenopappus*.

Genetic Tests

Methods.—Seeds collected during the summer of 1951 were germinated the following winter on moist filter paper in petri dishes and the seedlings grown in greenhouse pots. In spring these seedlings were transplanted to an outside garden. Ten plants of most of the collections were grown to maturity and the crosses indicated in Figure 21 attempted.

The plants were first tested for self-sterility by bagging portions of the inflorescence before anthesis. If seed failed to form in these bagged heads, it was assumed that the species was self-sterile.

Two methods were used in cross pollination: (1) the heads were bagged while in bud and after anthesis the pollen was blown or washed off and foreign pollen introduced by brushing an anther held in tweezers across the styles, and heads then re-bagged; (2) peripheral florets were emasculated, foreign pollen introduced, and unpollinated florets removed before rebagging. In either case, if seeds with embryos developed the cross was interpreted as a successful one. It was found, in rare instances, that what were thought to be carefully bagged heads of self-sterile plants set one or two seeds whether foreign pollen was introduced or not, and it is suspected that some of the taxa are not completely self-sterile. Hence, successfully formed embryos as indicated in Figure 21 may not be an entirely accurate indication of crossability. In most instances, however, the crosses represent formation of several mature embryos per head.

Results.—All species tested were found to be self-sterile or nearly so except *H. newberryi* and *H. scabiosaeus* var. *corymbosus*. In general, it seems that crossing between the several species and varieties tested, so far as embryo development is concerned, occurs readily. Unfortunately, time was not sufficient to grow the supposed hybrid seeds to verify these assumptions, but the seeds have been saved for future study.

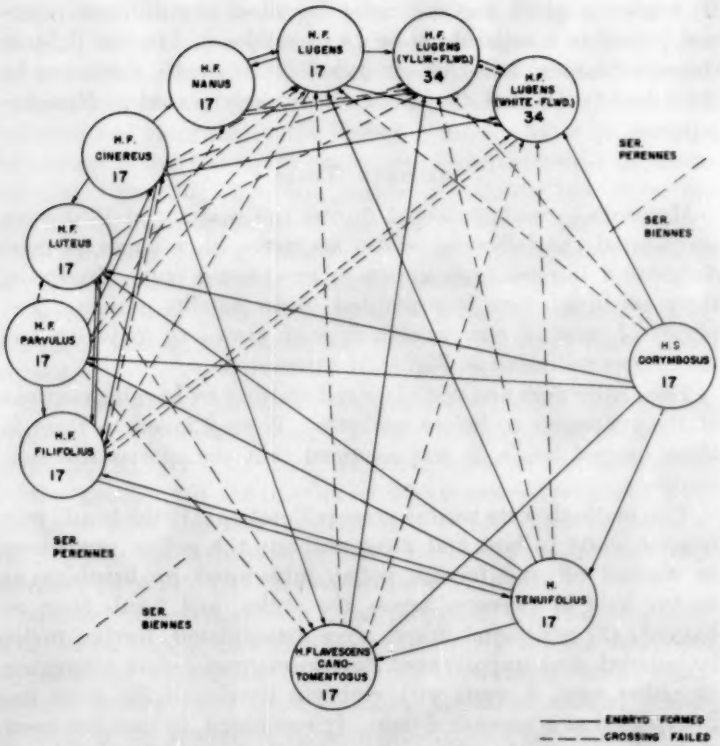


Fig. 21. Diagram of specific and varietal crosses attempted within *Hymenopappus*. Solid lines indicate successful production of mature seeds with embryos; dashed lines failure. Double lines show that the cross was attempted reciprocally. Arrows point to the female parent.

Morphology and Taxonomic Criteria

It is difficult to assign values to particular characters, for a distinguishing character in one group may be a highly variable one in another. This is especially true at the varietal level where distinctions are usually made on a combination of features. The characters listed below were useful principally in the delimitation of specific categories; however, application in some instances could be made at the infraspecific level.

Habit.—Species of Series Biennes are tall, mostly leafy-stemmed biennials; those of Series Perennes tend to be lower, less leafy perennials.

ROOT.—Biennial species have a single obconical tap-root which normally bears but one crown at its apex. Perennial species have a woody tap-root which, in older plants, bears branches with several to many crowns.

LEAVES.—Most of the species have pinnately compound leaves, although two species commonly have simple, entire leaves. The degree of leaf dissection and size of ultimate segments have been particularly useful in delimiting varieties.

INFLORESCENCE.—In all the species the inflorescence is a few- to many-headed cymose panicle. Biennial species usually have several leafy lateral branches which contribute to the many-headed inflorescence; perennial species are usually without leafy lateral branches, the inflorescence being composed almost entirely of peduncles produced from the main stem.

HEADS.—Radiate and discoid heads appear in species of both the biennial and perennial groups, the discoid type being much more common. In the discoid species the texture and size of the involucral bracts are often distinguishing.

COROLLA.—The shape of the disk corolla, particularly that of the throat, has proved significant in several instances, both at specific and infraspecific levels. Two principal throat types are found in the biennial species: funnelform throats in the species of the eastern United States, and campanulate throats in the central and western species. In general, funnel-form-throated taxa also have long narrow tubes; campanulate-throated taxa have shorter tubes. The perennial taxa all have campanulate throats. The size of the throat varies considerably in the *H. filifolius* complex, but when correlated with other characters serves as a convenient marker.

COROLLA COLOR.—This character is an important one and should be included on collection labels when possible. A number of taxa can be separated by this feature alone, thus making a comparison of several combined characters unnecessary. There are two common flower colors in the genus, yellow and white. The perennial species are nearly all yellow-flowered, but a few varieties of *H. filifolius* have white flowers or white-flowered races. The biennial species are principaliy white-flowered, but include three yellow-flowered taxa. In addition, one taxon (*H. artemisiaefolius*) may have a reddish or wine-colored corolla.

Pubescence.—With some exceptions, pubescence has not proved to be of much significance. In the perennial species a dense tomentum or woolly mat of hairs is usually found in the axils of the basal rosette leaves. The biennial species are without this dense tomentum or, if it is present, it is of a lesser amount. Within the species or variety the overall pubescence varies considerably, and it is suspected that this is a result of environmental influences in some instances. Seeds collected in the field from tomentose-leaved specimens of *H. filifolius* var. *lugens* (*Preece & Turner 2710*), when grown in the garden at Pullman, Washington, produced plants with nearly glabrate leaves. Glandular hairs are found on the corolla tube in nearly all species of *Hymenopappus*, but have been of practically no use in circumscription of species or varieties. On the other hand, achenial pubescence seems to be relatively constant, and has been used in combination with other characters to delimit certain taxa.

Achenes.—The achenes are basically alike in the genus, differing principally in size, degree of pubescence, and length of pappus. In most species the achenes are obpyramidal with four sides, but in some there is a tendency for them to be incurved and diagonally compressed, especially at the periphery of the heads.

Style branches.—The styles are essentially alike in all the species, having obtuse flattened lobes with distinct marginal stigmatic lines on the upper surface and papillose tips.

Measurements

Except in those taxa described as new, all flower measurements were made from dried specimens. Throat/lobe ratios were calculated by dividing the throat length by that of the lobe from the point of reflection (not the sinus). Since the number of florets in each head varies considerably, even on the same plant (earlier heads contain more florets than later ones), terminal heads and/or the first one or two successive ones were used for these counts. Obviously late-flowering specimens with abortive flowers and injured plants were excluded. Achene-pubescence was measured to the nearest tenth of a millimeter by use of an ocular micrometer. Measurements were taken

from those hairs at the middle of a corner of the achene. With some exceptions, achenial pubescence proved fairly constant in any one taxon.

Since leaf segmentation has frequently been useful in drawing varietal lines, especially in the *H. filifolius* group, a particular part of the leaf was needed for measurement so as to compare the various taxa uniformly. The terminal segment at the apex of the leaf has therefore been selected for the linear measurements used in the keys (but not in descriptions).

Leaf silhouettes were made in the following manner: Leaves were collected fresh and pressed flat. When dry, these were inserted between sheets of white paper and a soft lead pencil used to shade the top sheet so as to reveal the exact outline of the leaf below. This outline was then filled in with India ink and the pencil smudge erased.

Specific Concepts

In the present paper the natural units of *Hymenopappus* have been delimited by the combined information obtained from morphology, cytology, ecology, and geographic distribution. An attempt has been made to treat the taxa consistently with respect to their designation as species, variety, or population. In some instances distinct populations have been pointed out as perhaps worthy of varietal rank, but because of the complexities involved, and the further studies needed to delimit these groups properly, nomenclatural status has not been assigned.

The use of the term "variety" for infraspecific units follows the usage implied by the International Code of Botanical Nomenclature (1952, Article 14 and Appendix 3, Article C.5). The author believes this is desirable since the term has become ingrained in botanical usage and classification. In addition, the use of "subspecies" for the taxa here designated as varieties would not leave available a recognized term for the grouping of these infraspecific taxa, a course which has not been followed in this study but which may become advisable with accumulation of more information.

Generic Relationships and Taxonomic Position

The species of *Hymenopappus*, as here delimited, make up a

closely knit, natural group whose members are more similar to each other than to any known member of another genus. The total similarity of corollas, achenes, leaf patterns, and general aspect in the included taxa is truly remarkable, especially when one considers that the genus includes everything from perennial plants with chaffy receptacles and rayed heads to biennials with neither chaff nor rays.

Some workers (Hoffman, 1897; Rydberg, 1914; Johnston, 1923) have included various species of the genus *Hymenothrix* in *Hymenopappus*, mostly on the basis of pappus morphology, or other achenial characters. *Hymenothrix* was proposed by Gray (1849) to accommodate *H. wislizenii*, an annual species of southern Arizona, New Mexico, and adjacent Mexico. Subsequently four other species from the same general area were added to the genus by various authors. Heretofore, the chief character used to distinguish the two genera was the excurrent awn or midrib on the pappus scales of *Hymenothrix* as opposed to the included midrib on those of *Hymenopappus*. However, it was found that *Hymenothrix palmeri* may or may not have awns extending from its pappus scales and, consequently, it was thought that this situation destroyed the distinctions between the genera. Accordingly, Rydberg (1914) distributed the species of *Hymenothrix* in three genera: He recognized *Hymenothrix* as monotypic; established a new genus *Trichymenia* for one of the species (*H. wrightii*); and put the remaining species in *Hymenopappus*. Johnston (1923) accepted Rydberg's treatment stating, "I am following the only natural alternative of recognizing *Hymenothrix* and *Trichymenia*. The generic lines as here taken are very weak and those that maintain them must find their arguments in precedence and convenience."

There are several morphological characters which distinguish *Hymenopappus* from *Hymenothrix* (including *Trichymenia*), and so far as is known, the two genera are separated by discontinuities which are not bridged. Chromosomal studies should offer additional evidence bearing on this problem, but it is felt that the morphologic differences alone are sufficient to distinguish the two as genera, and it is doubted that they are even closely related. Inasmuch as it destroys the coherence of both groups, Rydberg's treatment is highly artificial. The

important distinctions between these genera are enumerated below:

HYMENOPAPPUS	HYMENOTHRIX
1. Disk corollas regular, the lobes all alike.	1. Disk corollas zygomorphic, the lobes unequal (inconspicuously so in *H. wislizenii*).
2. Leaves bipinnately compound to simple.	2. Leaves biternately or triternately compound.
3. Plants biennial or perennial.	3. Plants annual (?).
4. Corolla lobes (after anthesis) strongly recurved.	4. Corolla lobes erect or merely spreading, not recurved.
5. Pappus scales with medial nerve completely included.	5. Pappus scales with medial nerve extending to the apex or excurrent into a distinct awn.

The author has made no attempt to separate *Hymenothrix* from *Florestina* or other related genera; that is a problem for the future, but the exclusion from *Hymenopappus* of all species of *Hymenothrix*, and the retention of these species together in the same genus (including *Trichymenia*) seems sound on the evidence available at present.

Hymenopappus apparently has no immediate relatives within the Helenieae. The majority of the species of the genus are clearly derived from an ancestor with rays and chaff, perhaps not too unlike *H. newberryi*. Since such a species would not key to or fall naturally within the circumscription of the Helenieae, it would seem logical to look to other tribes for its relatives. In this connection, it is interesting to note that Hoffman (1897) in Engler and Prantl's world treatment of Compositae included *H. newberryi*, as the genus *Leucampyx*, in the tribe, Anthemideae, as did Gray (1877). Bentham and Hooker (1873)[6] also placed *Leucampyx* in the Anthemideae stating, "Genus evidenter *Anthemidi* quam maxime affine, different patria, receptaculo ut videtur parum convexo, achaeniorum magnitudine et forma, et styli ramis minus truncatis."

Thus it seems likely that *Hymenopappus* as a genus has its closest relationship with members of the tribe Anthemideae or perhaps some as yet uninvestigated member of the tribe Heliantheae (many of the characters of *H. newberryi* might place its ancestors here). This does not mean that the tribe

[6] *Leucampyx* was first published and credited to Gray by these authors, but no specific name was proposed.

Helenieae in general is not a natural group, but rather that *Hymenopappus* appears to be not as closely related to members of the Helenieae as to members of the tribes mentioned above.

Distribution, Ecology, and Possible Origin

Hymenopappus occupies an extensive area in the western and southwestern United States and central Mexico. The genus can be divided into two well marked geographical and morphological groups: Series Perennes, the principal members of which occupy the mountainous areas of the western United States and central Mexico, and Series Biennes, the principal members of which occupy the plains and lower areas to the east and southeast of the Rocky Mountains.

The species of Series Perennes appear to show, for the most part, a progressive adaptational trend toward xerophytism. The more primitive members of this series (see discussion below), *H. newberryi* and *H. radiatus*, have restricted distributions, and occupy more mesic situations (*Pinus ponderosa* to *Picea engelmannii* zones) than do the obviously more advanced taxa of the *H. filifolius* complex, the members of which occupy more xeric habitat types (*Pinus ponderosa* zone and lower).

Species of Series Biennes may, in turn, be grouped into two main morphological and geographical types: (1) a group of taxa having bipinnately dissected basal rosette leaves and corollas with campanulate throats, these taxa ranging from the central Great Plains to western Texas and Mexico along the eastern periphery of the range of Series Perennes; (2) a group of taxa having less dissected basal rosette leaves and corollas with funnelform throats, ranging along the Gulf Coastal Plain to Florida, and northward up the Mississippi Valley to Kansas, Illinois, and Indiana.

As in Series Perennes, the most primitive member of this group, *H. biennis*, is a rayed species. It occurs in the higher mountains of southern New Mexico and adjacent Trans-Pecos Texas, and commonly is associated with *Pinus ponderosa*, *Pseudotsuga taxifolia*, or *Picea engelmannii*. *H. biennis* seems to represent a surviving species or close relative of the ancestral stock which gave rise to the Biennes. The campanulate-throated members seem not to have migrated far from their

ancestral source, but have become adapted to more xeric conditions, developing (or retaining) bipinnately dissected leaves. The funnelform-throated groups appear to have branched off early enough from this ancestral biennial stock to retain less dissected, often simple leaves, perhaps indicating rapid spread and adaptation to more mesic situations to the southeast of the present-day Rocky Mountains.

Combining geographical, ecological, and morphological evidence with the apparent evolutionary trends of the major groups it is possible to suggest a plausible history of the genus as concerns speciation, migration, and present day distribution.

In order to understand the evolutionary trends in the genus it is necessary to reconstruct the appearance of the probable ancestral stock. This has been done by pooling all the assumed primitive characters now found in the various taxa. Such a procedure is justifiable on the assumption that the group is monophyletic and that the species existing today have retained some primitive characters while losing or modifying others. The critical part of this reconstruction is distinguishing between those characters which are primitive for the genus, and those that are derived. The following is a list of what the author considers primitive and corresponding derived characters of the genus *Hymenopappus*.

Primitive	*Derived*
1. Receptacle chaffy	1. Receptacle non-chaffy
2. Ray flowers present	2. Ray flowers absent
3. Root perennial	3. Root biennial
4. Leaves simple	4. Leaves dissected
5. Stem leafy	5. Stem subscapose
6. Inflorescence few-headed	6. Inflorescence many-headed
7. Achenes pubescent	7. Achenes glabrate
8. Involucral bracts mostly non-membranous	8. Involucral bracts mostly membranous
9. Pappus scales well developed	9. Pappus scales much reduced or absent
10. Receptacle large, convex	10. Receptacle small, nearly flat
11. Self-fertile	11. Self-sterile

From this tabulation, the reconstructed ancestral species of *Hymenopappus* should be, in general, a leafy-stemmed perennial with simple leaves, having a few-headed inflorescence, ray florets, and chaffy receptacle (see diagrammatic scheme of

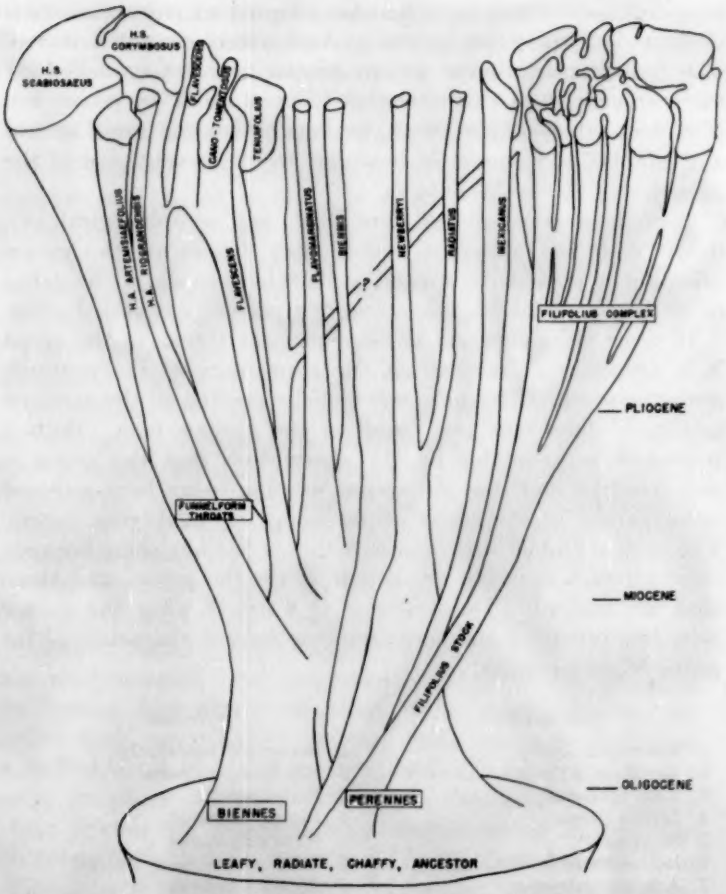


Fig. 22. Schematic representation of the suggested origin and evolution of present-day *Hymenopappus* species.

phylogeny, Fig. 22). No single species of present day *Hymenopappus* has all the primitive characters listed above, but *H. newberryi* retains seven of them (1, 2, 3, 6, 8, 10, 11), and is probably the least advanced or most primitive member of the genus.

The two most primitive members of the Perennes, *H. newberryi* and *H. radiatus*, and the most primitive member of the

Biennes, *H. biennis*, are restricted in their ranges, occupying the forested mountains of southern Colorado, east-central Arizona, and southern New Mexico (Fig. 24). These species (and those derived from them) seem not to have their immediate affinities with the present-day Composite genera of western North America; indeed, if past students of the Compositae were correct in assigning *H. newberryi* to the tribe Anthemideae, its nearest relatives should be in Eurasia, where most present-day members of the Anthemideae are concentrated (Bentham, 1873). Whether this is true or not, it seems likely that these species have come from the north via the Rocky Mountains. This is attested by the following facts:

(1) The most primitive members of the genus are associated with a number of temperate mesophytic species, perhaps representing relic members of the once more widespread Arcto-tertiary Flora.

(2) Clearly more reduced species have apparently diverged from a southern Rocky Mountain center westward, southward, and southeastward (it would be most difficult to read this speciation in a reverse direction, as this would call for progressive development of rays and chaff—characters which nearly all workers in the Compositae agree are primitive).

(3) Lack of closely related genera to the south (absence of such groups to the north can possibly be explained by the destruction of related genera, if such existed, by progressive climatic change since Oligocene time and the Pleistocene ice advances).

Thus it seems possible that the ancestral stock of present day *Hymenopappus* migrated southward down the uplifting Rocky Mountain chain in Oligocene time, possibly along with other members of the Arcto-tertiary Flora (Chaney, 1947). The Miocene epoch saw the break up of this ancestral stock into several well-developed lines. Biennial taxa developed and spread southward to central Mexico and eastward to southern Texas. The funnelform-throated species seem to represent the terminal members of this imagined expansion, and appear to have developed in Pliocene time, and spread secondarily from southern Texas, occupying the Gulf Coastal Plain and inland habitats of the upper Mississippi Valley (evidenced by

the considerable variability and presence of assumed primitive members in southern Texas; cf. *H. artemisiaefolius* var. *riograndensis*).

The campanulate-throated biennial species, as already noted, remained mostly peripheral to their supposed ancestral center, and have retained many of the characteristics of *H. biennis*. Specifically, it seems likely that *H. tenuifolius* became adapted to the arid plains east of the Rocky Mountains, possibly in Pliocene time, and has since remained associated with the grasslands of this region; while *H. flavescens* var. *cano-tomentosus* became adapted to the more southern intermontane xeric habitats of Arizona, New Mexico, and Trans-Pecos Texas.

Hymenopappus filifolius of the Perennes series is the most complex and widespread species of the genus. It is likely that its range, infraspecific variation, and complexity is a reflection of the climatic vicissitudes and geologic events of the region in which it is now located.

Pliocene time saw the development of extremely arid conditions in the Great Basin area west of the Rocky Mountains (Axelrod, 1948). Thus, one might visualize the spread of some ancestral *Hymenopappus filifolius* stock from a more mesic habitat type of southern Colorado and northern New Mexico to this newly formed desert basin. With the stimulus of aridity, rapid evolution may have occurred, as suggested by Stebbins (1952). It seems likely that once a trend toward xerophytism had become established, rapid evolution and diversification might occur, especially if the area occupied is one of much climatic change and geologic unrest. The situation in the present-day *H. filifolius* with its numerous, complex and intergrading infraspecific taxa was perhaps what Axelrod (1948; pp. 134, 135) had in mind when he made the following statement concerning Great Basin environments:

> Furthermore, under the impact of fluctuating Pleistocene climates these environments were in a state of continual flux. In such areas a wealth of new entities may have arisen in latest Cenozoic time, further differentiating from their mid-Pliocene ancestors. Many new forms may thus have evolved in latest Cenozoic time due to the selective influence of rapidly developing and fluctuating localized environments which became successively more narrowly limited in extent. This apparently accounts for the wide ecological diversification of these herbaceous types which show a high degree of adaptation in the utilization of geologically recent, highly localized habitats. Differentiation of the various cate-

gories has been limited largely by the genetic variability of the populations and by the diversity of localized environments. Nonetheless, the relatively short time that these highly-localized environments have been in existence may well account for the low degree of differentiation of many of the categories, and for the rapid evolution that is continuing today.

It seems likely that *H. filifolius* owes much of its infraspecific variation to such a history, along with that variation superimposed by subsequent hybridization and introgression.

There remains to be considered *Hymenopappus mexicanus* of the Perennes series. It apparently represents an early offshoot of the same reduced line. This species does not seem to have given rise to any other present-day taxon, though considerable variability is found in the many populations composing it.

In review, the author suggests the following history of the genus *Hymenopappus* based on the evolutionary trends as gleaned from the evidence offered by present-day morphology, ecology, and distribution (cf. Figs. 22, 23).

(1) Migration of an ancestral stock southward down the rising Rocky Mountains in the Oligocene Epoch.

(2) Separation of this stock in Miocene time into two main evolutionary lines, Biennes and Perennes.

(3) Rapid spread of reduced biennial species southeastward from the Rocky Mountains in Pliocene time with adaptation of the more distant members to coastal, somewhat mesic, habitats; populations closer to the parental source of the Biennes became adapted to relatively xeric grassland habitats.

(4) Ancestral reduced stock of *H. filifolius* became adapted to the newly formed desert basin west of the Rocky Mountains in Pliocene time, and, as a result of aridity, climatic, and geologic disturbance in Pleistocene time, the species produced many variable and intergrading infraspecific taxa which became widely distributed over the Rocky Mountains, Great Basin, and peripheral areas.

(5) Funnelform-throated biennial species have dispersed secondarily from southern Texas to the north and northeast in Pleistocene time.

(6) Present-day ranges show the confinement of primitive species to relatively high, more mesic habitats of the southern Rocky Mountains; advanced reduced species are widespread and occupy more xeric habitat types, except where secondary adaptation and speciation has occurred.

In addition to the broad outline given above, more specific information concerning ranges, ecology and, in some instances, possible origin has been given in the discussion for each of the various taxa concerned.

Acknowledgements

The author is especially indebted to Professor Marion Ownbey

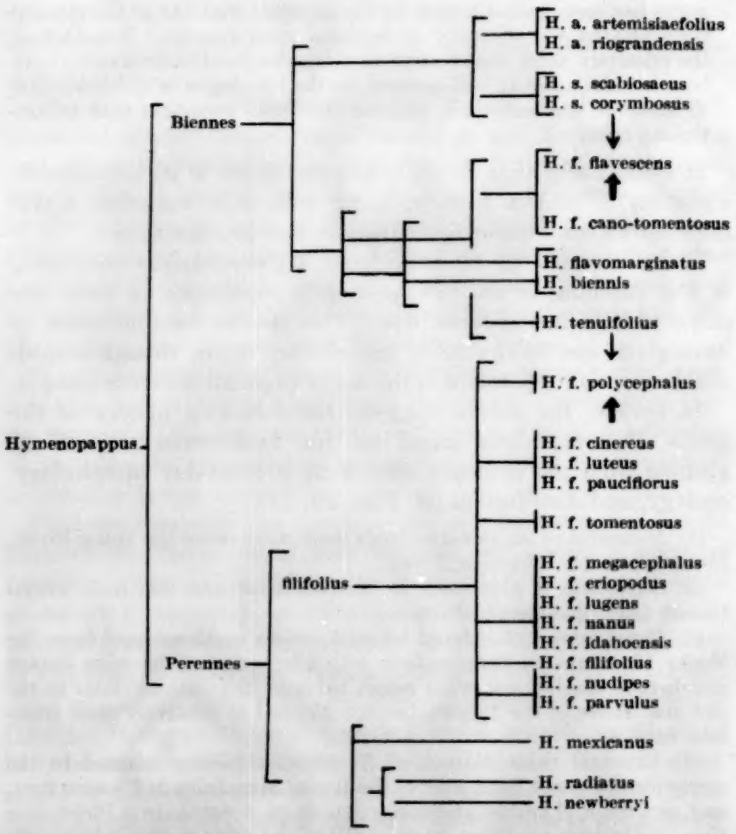


Fig. 23. Hypothetical relationships in *Hymenopappus*. Arrows point to taxa of possibly hybrid origin; tail of arrow refers to putative parents; width of shaft indicates the relative amount of characters contributed.

who suggested the problem and under whose direction the work was carried out. Grateful acknowledgement is also made to Rev. S. V. Fraser, Dr. Q. Jones, and Professor B. H. Warnock for seed collections; to Miss Nell C. Horner, Librarian of the Missouri Botanical Garden, and Professor L. H. Shinners for bibliographic information; and to Professor A. Cronquist for obtaining a photocopy of the original publication of *Hymenopappus scabiosaeus* and for his general interest in the problem.

(*To be continued*)

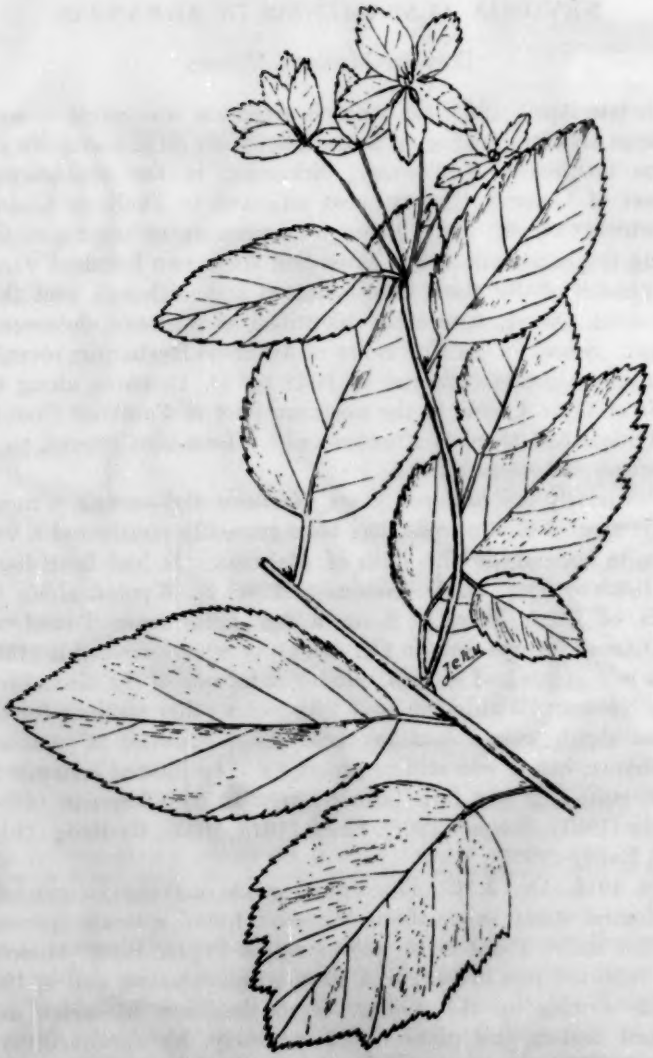
NEVIUSIA ALABAMENSIS IN ARKANSAS

DWIGHT MUNSON MOORE

IN late April, 1955, the writer's attention was called to some strange shrubs growing on a low sandstone ridge about six air-miles northwest of Conway, Arkansas, in the southeastern corner of Conway County, next adjacent to Faulkner County in which Conway lies. These were growing in some quantity along the sandstone ridge, extending some two hundred yards. Specimens of the plant were collected and, although past their blooming period, were easily identified as *Neviusia alabamensis* Gray. Search in the University of Arkansas Herbarium revealed four other sheets collected in 1925 by D. Demaree along the cliffs of Cove Creek, in the northern part of Faulkner County, and identified then as *Physocarpus*. These also proved to be *Neviusia alabamensis* Gray.

For nearly one hundred years, *Neviusia alabamensis*, a monotypic species of Rosaceae, has been generally considered a very definite endemic in the state of Alabama. It had been found in 1857 by Drs. R. D. Nevius and W. S. Wyman along the cliffs of Black Warrior River a few miles from Tuscaloosa, Alabama. It was sent to Dr. Asa Gray who described it (1858) as a new genus and species, naming it for one of the discoverers, Dr. Nevius. Within the next fifty years other stations for this same shrub were found in three other counties of northern Alabama, but it was still considered a very limited endemic for that state. It has thus been referred to by Chapman (1884), Mohr (1901), Harper (1906), Small (1913, 1933), Rydberg (1918), and Bailey (1935).

In 1918, Dr. J. C. Th. Uphof, while making an extended ecological study in southern Missouri, found a single specimen of this shrub about eight miles west of Poplar Bluff, Missouri. He reported this in 1921 in a German publication, and in 1922, while writing up the ecology of southeastern Missouri, mentioned finding this plant. Unfortunately, his specimens were destroyed before he got them back to U. S. herbaria from Holland, and little attention was paid to his find. As Dr. Uphof said, it was apparently an adventive, probably having been started from seed dropped by birds from Alabama or some



Neviusia alabamensis Gray.

FIG. 1. Map of southeastern United States showing location of collections of *Neviusia alabamensis* Gray at 1. Tuscaloosa (1857) (type locality); 2. other northern Alabama counties; 3. Poplar Bluff, Mo. (1918) 4. Cove Creek, Ark. (1925); Conway Co., Ark. (1955). Continuous line indicates margin of Coastal Plain.

hitherto unknown location in Tennessee. However, Harper (1928), in his *Catalogue of the Trees, Shrubs, and Vines of Alabama*, acknowledged the new discovery and mentioned it as the only place outside of Alabama where this plant had been found growing wild. In 1931 Fernald called attention to the relationship of this unique plant to its nearest relative, *Kerria*, in eastern Asia, and Bailey (1935) refers to it as very limited in Alabama. Palmer and Steyermark (1935) apparently did not consider the report of this one specimen sufficient for including it in their *Catalogue of the Flowering Plants of Missouri*, or they doubted Uphof's identification. Comparison of Uphof's drawing, here reproduced, with Gray's original drawing (1858) seems to leave no doubt as to his accuracy. Even as late as 1944, Cain refers to *Neviusia* as an example of extreme local endemism, showing it on a map as located only at Tuscaloosa.

With two Arkansas stations for this unusual plant, it seemed

logical to pursue further the reported find in southeastern Missouri. Search in July, 1955, in the region indicated west of Poplar Bluff, failed to reveal any evidence of the plant. However, this is not surprising, when consideration is given to all the changes of roads, fields, and other marks of 'civilization.' Furthermore, it may still be possible to find this or more plants of the same kind if it is sought in the spring when it would be in flower.

This now seems to make a very definite picture. By placing these locations on a map (fig. 1) showing the Mississippi embayment of the old Gulf Coastal Plain, it may be seen that the original find lay on the eastern side of the embayment, while the one from Missouri and the two from Arkansas are on the northwestern side of this embayment. In Alabama they are reported on sandstone, shale, and limestone. In Missouri it was reported on sandy loam, while in Arkansas the finds were both on sandstone outcrops. In all cases they appear to be on carboniferous or subcarboniferous formations. Geological evidence points to the fact that this particular area has been exposed above the encroachments of the sea since the late Paleozoic or early Mesozoic. This might lead us to believe that *Neviusia alabamensis* would be classified as an epibiotic, a relatively old relic species, according to Cain (1944), rather than a strict endemic which he would consider to be a relatively youthful species. At least, *Neviusia alabamensis* may no longer be considered to be strictly an Alabama endemic, but like a few other species it must be shared with other similarly located states.

Credit should be given to Mr. Marvin Lawson of Conway who had seen these plants there and recognized them as something unusual and who called them to the attention of the writer. Thanks are also extended to Dr. Hugh Iltis for his encouragement in the pursuit of this unusual find, and to Drs. Uphof and Harper who have aided in the location of some old records which have helped materially in getting this more nearly complete picture of *Neviusia alabamensis*. At Poplar Bluff, Mo., Mr. Frank Hearne was very coöperative in the attempt to relocate Uphof's station.—UNIVERSITY OF ARKANSAS, FAYETTEVILLE, ARKANSAS.

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HUMBOLDT AND AMERICAN BOTANY.[1]—"Alexander, that is a beautiful name. I seem to recall an earth-conqueror by that name. Do you wish to be a conqueror?" "Yes, Sire,—but with my head." So replied Alexander von Humboldt, aged eight, to King Frederick the Great. At the end of a long life there arrived in Berlin in 1857 an American, Bayard Taylor. He remarked, "I came to Berlin not to visit its museums, and galleries, its operas, its theatres, not to mingle in the gay life—but for the sake of seeing and speaking with the world's greatest living man—Alexander von Humboldt."

For Humboldt had seen both Bogotá and Baltimore, had conversed with Indian tribes and that student of Indian vo-

[1] HUMBOLDT. THE LIFE AND TIMES OF ALEXANDER VON HUMBOLDT, 1769–1859. Helmut de Terra. Alfred A. Knopf, N. Y. i-xvi, 1-386, i-ix. 8 plates, 3 maps. 1955.

cabularies, Thomas Jefferson, had climbed many of the highest peaks in tropical America and studied their faunas and floras. The historian George Bancroft wrote, "Humboldt was always the friend of young America."

The latest biography of "the greatest scientific traveller who ever lived," as Charles Darwin characterized Humboldt, has just been written by the geographer, Dr. Helmut de Terra, and beautifully produced by Alfred A. Knopf. The author has turned over materials that have long slept in Marburg and Paris, as well as the familiar sources in this country, but it is rather of some adjacent pastures still fallow that I should like to direct attention.

In 1804 at the age of thirty-five Humboldt paused in this country for eight weeks en route from Cuba to Paris, that is, at the conclusion of his great hegira to tropical America. In Philadelphia Humboldt particularly visited Prof. Benjamin Smith Barton, Benjamin Rush, and Charles Willson Peale. Peale's Philadelphia Museum, the largest of its kind in the New World, tremendously interested the young Humboldt.[2] He spent three weeks at Jefferson's Monticello, talking, walking, going over many matters of mutual concern. He spoke to Jefferson of having Congress purchase the museum amassed by Peale and thus establish a national collection. It was late May when the party of six, conducted by Peale, set out for Baltimore and Washington by coach. The other four were Aimé Bonpland—familiar to botanists for the abbreviation "H. B. K." which trilogy records the part played by the nephew of Humboldt's former tutor, Karl Sigismund Kunth, who did not accompany Humboldt and Bonpland—, Don Carlos Montufar of Quito, Dr. Anthony Fothergill,[3] and the Rev. Dr. Nicholas Collin.[4] The pilgrimage was not without its speechless moments. Peale's "dental bridge having broken, he rushed out to look

[2] For the tragic fate of Peale's historic specimens, another 'short chapter in the history of human stupidity,' see Thomas Barbour, A Naturalist's Scrapbook, 91–97. 1946.

[3] Anthony Fothergill (1733–1813), M. D., nephew of John Fothergill, came to America about 1803. Cf. R. Hingston Fox, Dr. John Fothergill and His Friends, 131–132. 1919.

[4] Nicholas (or Nils) Collin (1746–1831), student at Upsala, who arrived at Penns Neck, N. J. in 1778 and became rector of Swedish Churches in Pennsylvania. Aside from collecting seeds and plants and sending them to his native Sweden, he was interested in lead-glazing, philology, colonial history, climatology, etc. Cf. Th. Krok, Biblio. Bot. Suecana, 131, 1925; G. G. Simpson, Amer. Philos. Soc. 86: 130. 1942, and W. J. Bell Jr., Early American Science, 4, 15, 1955.

for a gunsmith to borrow tools to repair it. For one who had mounted the skeleton of a mammoth, this was a fast and easy job. Luckily he carried a few pieces of gold in his pocket, and so managed to mend his artificial teeth in time to rejoin the company for the rest of the evening."

Dinner at the Executive Mansion, visits with the first architect of the new capitol in Washington, Dr. William Thornton,[5] a conference with Secretary of the Treasury, Albert Gallatin, and a boat trip down the Potomac to Mt. Vernon (where now only Washington's negro body servant lived to tell his master's story first-hand), filled his days and evenings. Of Bonpland, then twenty-nine years of age, we should particularly like to know more, but he was eclipsed by Humboldt's overwhelming importance and handicapped by his inability to converse in English. The two visitors called on Henry Muhlenberg at Lancaster and the "American Linnaeus" packaged 160 grass specimens for Humboldt to compare with Michaux's collections at Paris. Humboldt's letter, not mentioned by de Terra, is of special interest to the botanist, it reads:

My dear and honored friend,

I use these last moments before my departure tomorrow, to express once more my heartfelt thanks to you for the great kindness which you showed me and my friends in Lancaster. Your grasses and your kind letter have come to hand and I promise to let you know Michaux's names for them. Bonpland commends himself to you with gratitude for your kind remembrance. Yesterday he had a delightful noon with your brother the worthy General. Remember me to the good Ellicott[6] and Mr. William Barton.[7] We saw the Hamilton garden with astonished delight.

Yours
most gratefully
Humboldt[8]

Philadelphia
the 27th June 1804

[5] William Thornton (1761–1828), M. D., a close friend of Jefferson, who evidently owned a set of plant drawings. He was a founder and one-time curator of the Columbian Institute for the Promotion of Arts and Sciences. Cf. E. M. Betts, Thomas Jefferson's Garden Book, 1766–1824, 398 *et passim*, 1944.

[6] Andrew Ellicott (1754–1820), civil engineer, who while laying out state boundaries collected plants unfamiliar to him. A few of these are preserved in the B. S. Barton Herbarium (ANSP). Cf. W. J. Bell Jr., *op. cit.*, 55–56.

[7] William P. C. Barton (1786–1856), who succeeded his uncle, B. S. Barton, as professor at the University of Pennsylvania. Cf. F. W. Pennell, Bartonia no. 21: 45. 1940.

[8] Paul A. W. Wallace, Muhlenbergs of Pennsylvania, 313. 1950.

Thus we have one more distinguished visitor to the "Woodlands"! Naturally it is of particular interest to this reviewer to note that Frederick Pursh was head gardener at Hamilton's estate at the time of Humboldt's visit. When is some member of the Philadelphia Botanical Club reconstructing William Hamilton's guest book? From the good beginnings made by Sarah P. Stetson[9] and others this is now a practicable project.

Audubon's friend and associate, Rev. John Bachman of Charleston, was present at the dinner given in honor of Humboldt at Peale's Museum. Bachman was barely fifteen at the time and was probably invited through the influence of Alexder Wilson.

> the two Bartrams, Wilson, the ornithologist, Lawson, his engraver, George Ord and a few others . . . Few speeches were made and those were short—there was no formality . . . Humboldt was then, as he was afterwards, in every society, "the observed of all observers" . . . [Bachman] saw him every day during the few days he remained in Philadelphia. He inserted my name in his note-book, and for the last sixty years we corresponded at long intervals.[10]

But when Humboldt finally sailed in July aboard the frigate *Favorita* down the Delaware for Bordeaux it was of Jefferson and those delightful weeks at Monticello that he recalled with special pleasure. It is not easy thoroughly to assay the influence of Humboldt's visit on Jefferson's great plan for the exploration of the West, so well advanced by the nearly completed expedition of Lewis and Clark, but it is certain that Humboldt's bold approval of Jefferson's aims gave encouragement to what was not a wholly popular program at the time.

Soon Humboldt's familiar pictorial diagram of Chimborazo demonstrating the zonation of vegetation "corresponding with its progress in different latitudes" was used as the frontispiece of a botany text published in 1829 by the vice-principal of Troy Female Seminary, Mrs. Almira H. Lincoln. Her *Familiar Lectures in Botany* enjoyed a sale of more than 275,000 copies in the succeeding forty years in the higher schools and academies of this country.

[9] Penna. Mag. Hist. Biog. 73: 26–33. 1949. Cf. also Thompson Westcott, Historic Mansions and Buildings of Philadelphia, 415 *et seq.* 1877; John T. Faris, Old Gardens in and About Philadelphia, 150 *et seq.*, 1932, but use with caution; J. Ewan, Proc. Amer. Philos. Soc. 96: 603–605. 1952.

[10] F. H. Herrick, Audubon the Naturalist, 2: 284–285. 1917.

Humboldt's American contacts continued throughout his lifetime. When Balduin Möllhausen, topographer and artist to Whipple's Pacific railway survey, visited Berlin with a consignment of animals for the city's zoo and paid a call on Humboldt, he met the daughter of Humboldt's valet. Later as Möllhausen crossed New Mexico with Whipple's party he wrote long love letters to Alexandra Caroline Seifert. It is generally recorded that Dr. John M. Bigelow was the botanical collector on Whipple's survey, but we find Möllhausen, in de Terra's words, "laden with plant and rock specimens for Humboldt to study." This Möllhausen material, which may represent authentic duplicates of species described from Bigelow's collections, may yet come to light, The diary of Dr. C. B. R. Kennerly, physician and zoologist to the survey, preserved in the Division of Manuscripts, Library of Congress, may hold the answer to this riddle. This is the Möllhausen called the 'German Cooper' for his immensely popular Indian love stories, travel lore, poetry, and some eighty novelettes![11]

Fremont spread Humboldt's fame in this country. Using extensively and taking inspiration from Humboldt's writings, Fremont was warmed by the praise accorded his Report. Alas! the argonauts who drank the bitter waters of the 'Humboldt Sink' in the rush for gold had little praise for either Fremont or the man he honored. Latin America preserves many witnesses of its appreciation for Humboldt. Bolivar and Humboldt stand side by side not only as twin peaks in the high range above the beautiful city of Merida but in the hearts of her patriots. Bolivar, to whom Humboldt gave encouragement, said that the "learning" of his friend had "done America more good than all the conquerors." Mutis, pupil of Linnaeus, and Humboldt and Bonpland worked in adjoining houses in Bogotá, and Mutis's biographer, A. Federico Gredilla, quotes long letters that passed between them.[12] We are still in desperate need of a biography in English of this great figure, whose library and collections of plant drawings were said to be second only to those of Joseph Banks. Sir Robert Schomburgk's explorations

[11] Möllhausen's contacts with John Xantus are interesting in this connection. Cf. H. M. Madden's Xantus: Hungarian Naturalist in the Pioneer West, 72, 238, 1949.

[12] Supplementary to Sprague's paper of 1926, cited by de Terra, cf. A. Dugand, Rev. Acad. Colomb. 9 (35): 210–213. 1954.

in Guiana keenly interested Humboldt, and he was again delighted when Prince Adalbert of Prussia's *Travels* in Brazil were translated by Schomburgk. In a preface Humboldt prepared for the English edition, he remarked, "if human civilization, which is making such giant strides in North America, should ever penetrate into these fastnesses (a hope which St. Basil calls 'day-dreams of man'), the structure of this great net of rivers, from north to south, may open channels of communication such as are unknown in any other part of the world."

Humboldt was a prodigious worker: in his early sixties he was working simultaneously on the final volume of his *histoire de la geographie* of America, completing his Asiatic studies—he had travelled 9600 miles through Asiatic Russia by coach in twenty-five weeks—and was planning the first volume of his great synthesis—now seldom read—entitled *Cosmos*. His writings exceeded in bulk those of any contemporary naturalist, rivalling Buffon and Leibnitz. His later writings were ponderous and at times repetitious; Arago, the physicist, had, in fact, insisted that Humboldt really did not know how to write a book, but that he wrote endlessly, and the result was not a book "but a portrait without a frame." The Scot, William Macgillivray, composed a useful resume of his travels and researches which went into a second edition. Corresponding and writing, the "Prometheus of our time" worked on, meeting American visitors, as when Prof. Benjamin Silliman of Yale visited him in 1851, and parrying with some over-zealous investigators: in 1843 a Dresden anatomist requisitioned Humboldt's skull upon hearing of his illness! Of that skull-duggery I know no more.

"I used to admire Humboldt, now I almost worship him," wrote Charles Darwin to his teacher Professor Henslow. Darwin insisted that his entire career was a consequence of his reading Humboldt's *Narrative of Travels*. The botanist Berthold Seemann said that "by his glowing descriptions of tropical scenery" Humboldt "did more than any one living to encourage that desire for the exploration of equinoctial regions, to which we owe . . . directly the elaborate works of Martius, Griffith, Blume, and other botanists of eminence." Humboldt was the fillip of Louis Agassiz's trip to Brazil. Prescott wrote that he was guided "by the light of his researches" and added that he

missed Humboldt's hand in his study of Peru which lay just beyond Humboldt's fields.

Dr. de Terra's biography is a highly successful portrait (with a frame!) done in sepia with plunging strokes. This biography does not intend to be exhaustive as the good index will quickly demonstrate. There is still a genuine need for a full and documented biography along natural history lines, dressed for its immense potential reference value but blind to Brentano's show window. This unborn biography will integrate from the rich *reliquiae* of Humboldt letters around the world, identify their personalia, trace the intercourse across the Atlantic, from amateur to mentor and back again, all arrayed at finger-tip accessibility by a complete index. The botanical collector Benedict Roezl discovered a new lily in California in 1869 and as a centennial gesture it was named for Humboldt. How fitting that Humboldt's second centennial should be marked by an Olympian biography. Shall it be called "Prometheus Unbound"?—JOSEPH EWAN, TULANE UNIVERSITY, NEW ORLEANS, LA.

ASCLEPIAS SYRIACA VAR. KANSANA IN NEW YORK STATE.—At the time of the 1952 meetings of the Botanical Society of America in Ithaca, New York, one of the local field trips planned for the Ecological Society included a stop northeast of Geneva on the east side of Seneca Lake. In the waste ground bordering the road was an extensive stand of *Asclepias syriaca* L. All gradations were observed from the essentially plain-surfaced fruits of forma *inermis* to the spiny-fruited var. *kansana* (Vail) Palmer & Steyerm. The collection data for the plants referred to var. *kansana* are "open ground bordering ditch along east side of highway 96 A, northeast of Geneva, on east side of Seneca Lake, Seneca Co., New York, September 11, 1952, *Steyermark & Swink 74625*." The range given for this spiny-fruited variety in Gray's Manual, eighth edition, is "Ia., Neb., Mo. and Kans." While Woodson in his recent monograph of the genus (Ann. Mo. Bot. Gard. **41**: 105–108. 1954) does not consider var. *kansana* to merit taxonomic rank, he does acknowledge the fact that the plants of the western states are *predominantly* spiny-fruited, while those of the eastern states

are *predominantly* smooth-fruited (loc. cit. p. 108, text and footnote). He relegates their status, however, to races and clines. Dr. Woodson's careful monograph notwithstanding and with our highest admiration for this work, the fact still remains that the field worker and local botanist, examining the two extremes of the fruit, one from the west with the spiny processes conspicuous, the other from the east nearly or quite plain-surfaced, are impressed by the *constancy* and *prevalence* of the spines or lack of them, depending upon the geographical location. The student and local botanist in Missouri and Kansas encounters the spiny-fruited type practically all the time, whereas in the eastern states the excessively spiny-fruited type is practically unknown. Since this morphological character can be combined to a certain degree with a circumscribed range, it does not seem to the present authors inappropriate to maintain varietal status for the predominantly western spiny-fruited var. *kansana*. If the spiny-fruited plants were found to be everywhere within the range of the smooth-fruited or less spiny types, there would be no point in maintaining a geographic status for the spiny-fruited plants. One expects to find every kind of intergradation where the boundaries of the one type pass over into those of the other, but that should not mitigate against the recognition of the two varieties, at least from the standpoint of a convenient category or name for purposes of identification. Also from the geographical standpoint, it would appear proper to retain taxonomic recognition of var. *kansana*. In addition to the single station for var. *kansana*, cited above for New York state, a new eastern record, the authors observed the spiny-fruited type in various parts of northern Illinois and Indiana. If the var. *kansana* is maintained, its range should be extended to include the states of Illinois, Indiana, and New York.—Julian A. Steyermark and Floyd A. Swink, Chicago Natural History Museum and College of Pharmacy, University of Illinois.

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